PARADOXICAL PREFERRED BODY TEMPERATURES OF TWO ALLOPATRIC *HOPLODACTYLUS MACULATUS* (REPTILIA: GEKKONIDAE) POPULATIONS FROM NEW ZEALAND

M.D. TOCHER

Department of Zoology, University of Canterbury, Private Bag, Christchurch, New Zealand.

(Received 4 May, 1992; revised and accepted 8 July, 1992)

ABSTRACT

Tocher, M.D. (1992). Paradoxical preferred body temperatures of two allopatric *Hoplodactylus maculatus* (Reptilia: Gekkonidae) populations from New Zealand. *New Zealand Natural Sciences* 19: 53-60.

A comparison of preferred body temperature (PBT) was carried out on two isolated *Hoplodactylus maculatus* populations from climatically distinct locations. Seasonal and acclimatory effects on PBT were determined. The PBT of the cooler climate Craigieburn geckos was elevated by 2-3°C with respect to Banks Peninsula geckos for field collected (summer and winter acclimatized) animals. Interpopulation differences disappeared following laboratory acclimation implying a non-genetic basis to the difference in acclimatized geckos. However the finding of a higher PBT in the cooler-climate population is noteworthy and is somewhat paradoxical in light of previous reptilian studies where PBT has been traditionally linked with degree of thermophily.

KEYWORDS: preferred body temperature - New Zealand - Gekkonidae - *Hoplodactylus maculatus* - climate.

INTRODUCTION

Behavioural thermoregulation in reptiles generally involves basking, postural adjustments and exploiting favourable microclimates (see Dawson 1975 for review). Behavioural manipulation of the body's thermal flux allows reptiles to maintain body temperature within a narrow range during activity (Bartholomew 1982). These levels of body temperature are referred to as 'thermal preferenda' or 'preferred body temperatures' (PBT). PBTs are often similar between congeners that occur in markedly different climates, but may differ substantially in sympatric species of different genera (Licht *et al.* 1966, Bartholomew 1982).

There are indications that several reptile species have two separate temperature preferences depending on their activity state; a lower body temperature when foraging, and a much higher one when basking. This has been shown for certain terrapins (Brattstrom 1965, Heatwole 1970, Werner 1972) and indicated for several geckos (Werner 1965, 1966, Bustard 1967, Heatwole 1970, Werner & Whitaker 1978). Heatwole (1970) suggested that 'activity - dependent thermal compartmentalisation' of activities may be common in lizards, the PBT of a species varying with such activities as foraging, digestion, defecation, breeding and resting.

Thermal compartmentalisation has been implied in nocturnal *Hoplodactylus* sp. (Hardy 1971, Werner & Whitaker 1978) and thus the definition of PBT becomes 'ambiguous'. *H. maculatus* are known to forage nocturnally at body temperatures of approximately 10-13°C (Werner & Whitaker 1978) and about 7°C (Dawbin 1962). Hardy (1971) found that *H. maculatus* had a distinct preference for a body temperature of 33°C in a thermal gradient and found no obvious difference between PBT during day and night. Therefore, from these observations it appears *H. maculatus* forages at a low body temperature at night, but if 'given the opportunity' would raise its body temperature to a much higher level.

Hoplodactylus maculatus observed in the field bask 'indirectly' during the daytime, moving from deep retreats (within rock crevices), as the temperature increases, to more exposed sites (Werner

& Whitaker 1978, and pers. obs.), presumably in order to increase body temperature. Diurnal thermoregulatory behaviour has also been observed in the Australian gecko *Gehyra variegata* (Bustard 1967) and the gecko *Ptylodactylus hassaequistii* (Werner 1965, 1972, Arnold & Gallagher 1977) and is thought to enhance digestion efficiency (Bustard 1967).

Difficulties with the concept and definition of 'preferred body temperature' for other lizard species has lead to several conflicting findings. Significant differences have been recorded between body temperatures measured in nature and those obtained in laboratory experiments (Licht *et al.* 1966, McGinnis 1966, DeWitt 1967) and considerable seasonal variation has been recorded between PBTs. Seasonal variation is most evident in nocturnal thigmotherms (Pianka & Pianka 1976), but has also been recorded in diurnal heliotherms such as two species of *Sceloporus* (Mayhew 1963, McGinnis 1966) and the European lizard *Lacerta vivipara* (Patterson & Davies 1978, Van Damme *et al.* 1986, 1987). PBT can be modified by various factors, including feeding (*ie.* digestion, Regal 1966, Cogger 1974, and pers. obs.), or previous temperature acclimation (Wilhoft & Anderson 1960, Licht 1968, Kaufmann & Bennett 1989).

The linkage of physiological function to behaviourally controlled body temperature has been particularly well documented in lizards (Dawson 1975, Bartholomew 1982). Reptilian physiological functions that have been associated with preferred body temperature include ATPase activity of myosin (Licht 1964, 1967) and heat suppression of resting metabolism. An example of the latter is that the lizards *Gerrhonotus multicarinatus* and *Eumeces obsoletus*, with PBTs of 30°C and 34.5°C respectively (Licht 1964), undergo heat suppression of resting metabolism when warmed to 40°C (Dawson 1960, Dawson & Templeton 1966). In contrast, the thermophilic lizards *Dipsosaurus dorsalis* and *Crotaphytus collaris* with PBTs of 38.4°C, do not suffer such suppression until body temperature reaches levels in excess of 45°C (Dawson & Bartholomew 1958, Dawson & Templeton 1963). Other functions coupled with PBT include resistance of testicular tissue to thermal damage (Mellish 1936, Licht 1965), sensitivity of the inner ear to sound (Werner 1972), maximal twitch tension of skeletal muscle (Licht 1964, Licht *et al.* 1969), rate of digestion (Cowles & Bogert 1944), heart rate (Dawson 1967, Templeton 1970) and the Q_{10} of other rate functions (see Dawson 1975 for review). Therefore, reptiles appear to have a species-specific range of body temperatures, maintained largely by behavioral means, where various bodily functions are most efficient.

Whether similar species of lizards living in thermally distinct environments show genetic adaptation of thermophysiology has frequently been debated (Patterson & Davies 1978, Van Damme *et al.* 1986, 1987, 1990). Bogert (1949) developed the static view of thermophysiology, in which he suggested that 'thermal preferences' (his term for activity temperature, which correlates with physiologically optimal temperature; Dawson 1975) are "...fixed by heredity...at the species level and...closely related species have similar...body temperature preferences" (Bogert 1949).

The static view of thermophysiology is based largely on studies of desert reptiles (Bogert 1949, Brown & Feldmuth 1971, Crowley 1985) and emphasizes that thermophysiology is evolutionarily conservative and thus relatively insensitive to directional selection. This view is derived from the generalisation that aspects of the thermophysiology of lizards typically show little differentiation within or among closely related taxa from climatically distinct habitats. Because desert reptiles adjust their thermoregulatory behaviour to local environmental conditions, geographic variation in body temperatures, and presumably physiological performance, during activity is minimal.

In contrast, the labile view, based largely on more recent studies of tropical iguanid lizards (Huey 1982, Van Berkum 1986, Tsuji 1988), argues that thermal physiology does respond readily to directional selection in some taxa.

Hoplodactylus maculatus has recently been informally recognised as a species complex of seven species (Hitchmough pers. comm.). Populations of *Hoplodactylus maculatus* exist in many varied habitat types and experience heterogeneous climatic regimes throughout their distribution range of sea level to 1 400 metres a.s.l. Therefore, *H. maculatus* offers an excellent opportunity to investigate these two opposing views on thermal physiology; static versus labile. Geckos in this study were collected from Castle Hill, Craigieburn, an alpine site 900 m a.s.l. at a latitude

of 43°09'S, and Banks Peninsula, a lowland site 50 m a.s.l. at a latitude of 46°19'S. If thermal physiology in *H. maculatus* is 'labile', differences in PBT are expected between Craigieburn and Banks Peninsula geckos under identical laboratory conditions, with Craigieburn geckos showing a relative lowering of PBT and subsequent lowering of optimal temperature for physiological performance. Craigieburn geckos come from a higher altitude site which is on average 6°C cooler than Banks Peninsula (Christchurch Meteorological office data). In particular, Craigieburn geckos experience longer more severe winters, with prolonged snow cover (see Tocher 1992 for a detailed climatic comparison of these sites). If on the other hand, the static view holds, then the PBT characteristics of each population would be similar.

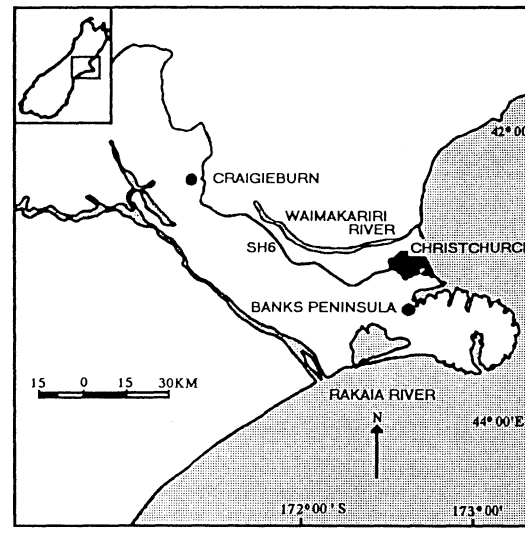

Figure 1. Locality map of gecko collection sites (Craigieburn and Banks Peninsula).

MATERIALS AND METHODS

STUDY SITES AND ANIMALS

Geckos were collected by hand from rock outcrops in the Castle Hill Basin (Craigieburn) approximately 80 km inland from Christchurch, and from Teddington on Banks Peninsula, New Zealand (Fig. 1). Only adult males (5.0-10.0 g with a definite swelling at the base of the tail) with complete tails were collected and used in experimentation.

EXPERIMENTAL PROTOCOL

Geckos were collected in mid summer (January) and mid winter (July) 1991 from each site. Geckos collected in summer were divided equally, with respect to weight, into three acclimation groups and a further nine geckos were used to determine the PBT of geckos fresh from the field. This latter group were exposed to summer laboratory temperatures prior to experimentation and preferred body temperature was measured no more than 10 days following collection from the field; acclimatized values (Bullock 1955). Three acclimation procedures were used: geckos were acclimated to 5°C for one month, 5°C for four months, or 25°C for one month. During acclimation, geckos were fed a yeast-honey mixture with water *ad libitum* and subjected to a 12L:12D light regime. PBT was determined for nine geckos from each treatment, except Craigieburn geckos acclimated to 5°C for four months where five geckos were used.

All geckos were starved for at least 7 days prior to experimentation to ensure they were in a post-absorptive state. Feeding and subsequent digestion are known to affect PBT in lizards (Regal 1966, Cogger 1974).

Measurements were taken between 1200 h and 1800 h, at which times animals were likely to be in a 'thermoregulatory state' (*ie.* animals are known to bask, either in the open or within sheltered crevices during daylight hours; Werner & Whitaker 1978).

Two darkened, 90 cm x 10 cm thermal gradients were used for all tests. The gradient consisted of a single aluminium plate (0.5 cm thick), one end covered with ice packs, and the other heated by a 100 W light bulb. The light bulb was housed beneath the aluminium plate inside a ventilated box. A constant substrate gradient of 5°C to 70°C was created after the temperature of the device had stabilised. Gradients were housed in a 15°C constant temperature room.

Animals were chilled to 5°C for 2-3 h before being placed in the centre of the darkened gradient. This ensured that animals would actively seek to increase their body temperature to a 'preferred level'. After 45 min (an arbitrary value, deemed adequate for geckos to achieve PBT during pre-

liminary trials) animals were removed and their body temperatures measured with a fast reading thermocouple inserted into the cloaca. Care was taken not to alter the animals' body temperature through handling.

ANALYSIS

Preliminary analysis for five treatments where body mass was known showed no significant correlation between PBT and body mass ($P > 0.05$). Thus observed PBT values were not dependent on the size and body weight of the geckos. Subsequent analysis comparing PBTs among populations and treatments employed analysis of variance (ANOVA). Variances were tested for homogeneity using regression analysis.

RESULTS

Variances for both the acclimatization and acclimation ANOVAs were homogeneous ($F = 0.70$ and $F = 0.85$ respectively; both $P > 0.05$).

ACCLIMATIZATION

For acclimatization treatments a significant difference was shown between populations (ANOVA; $F = 10.24$, $P < 0.005$), Craigieburn geckos having higher mean PBTs for both seasons (Fig. 2). The effect of season (*ie.* summer versus winter collection) was also significant (ANOVA; $F = 4.75$, $P < 0.05$), and was similar in both populations (ANOVA; $F = 0.19$, $P > 0.05$, no significant interaction effect); winter field conditioning produced a lower PBT (difference from summer, 1.96°C and 1.3°C for Craigieburn and Banks Peninsula respectively).

ACCLIMATION

Exposure to the three acclimation treatments resulted in a non-significant population difference (ANOVA; $F = 0.38$, $P > 0.05$), but a strong treatment effect (ANOVA; $F = 14.83$, $P < 0.001$). This treatment effect was similar in both populations (ANOVA; $F = 0.65$, $P > 0.05$; no significant interaction effect, Fig. 2).

Fig. 2 clearly differentiates between 5°C and 25°C acclimation treatments, although population differences are indistinguishable as indicated by ANOVA. PBT following 25°C acclimation is similar to that of summer collected animals, and similarly, winter acclimation produced PBTs similar to those following 5°C acclimation.

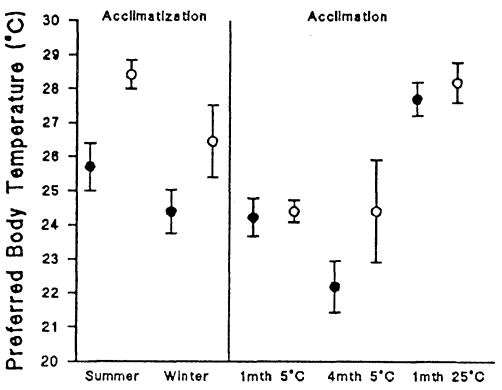

Figure 2. Preferred body temperatures of Craigieburn (o) and Banks Peninsula (●) geckos following collection from the field, or laboratory acclimation (mean SEM, n value as shown).

DISCUSSION

Results from this study lend some support to the labile view of thermophysiology. Geckos originating from Craigieburn maintain a higher PBT than Banks Peninsula geckos, indicating that PBT is subject to directional change under differing thermal environments in *Hoplodactylus maculatus*.

The absolute mean PBT of Craigieburn geckos was consistently above that of Banks Peninsula geckos (Fig. 2) although only significantly for acclimatized treatments. Interpopulational differences disappeared following laboratory acclimation suggesting the differences in field acclimatized geckos are not genetically based. The finding of a higher PBT in Craigieburn geckos appears paradoxical; the mean daily temperature at Banks Peninsula is on average 6°C higher, with less severe winters, than Craigieburn (Tocher 1992). Thus, under identical laboratory conditions I expected a lower PBT in acclimatized Craigieburn geckos and a consequent lowering of optimal temperature for physiological performance. Similar studies have emphasized the relationship between heat resistance and PBT (Dawson 1960, Dawson & Templeton 1966) and the relationship between PBT and degree of ther-

mophily (Dawson & Bartholomew 1958, Dawson & Templeton 1963), thus the higher PBT of Craigieburn geckos, collected from a cooler climate, was a somewhat unexpected result in light of these previous studies.

The presence of acclimatization (*ie.* change in PBT with season) evident in both populations implies a degree of flexibility in PBT. By contrast, standardised laboratory conditions failed to produce a PBT distinction between the *H. maculatus* populations. However, treatment did have a significant effect, with cold acclimation (5°C for one and four months) producing a lowering of PBT, whilst warm acclimation (25°C for one month) produced higher PBTs in both populations (Fig. 2). Kaufmann & Bennett (1989) also found a lower PBT in cold acclimated *Xantusia vigilis* as compared to warm acclimated animals.

The effect of acclimation was similar to that seen in acclimatized geckos (*ie.* both summer and 25°C acclimated geckos show a higher PBT when compared to winter or cold acclimated geckos). Long term acclimation resulted in a higher mean PBT for Craigieburn geckos relative to Banks Peninsula, in line with observed elevations in acclimatized geckos. This elevation was not significant ($P > 0.05$), however, the consistency of this result implies some adaptive value to maintaining a high PBT in cool climate areas.

Why then do field-acclimatized geckos from the cooler Craigieburn site have PBTs 2-3°C higher than those from Banks Peninsula? One possible explanation is that prevailing weather conditions prior to collection influenced the observed PBT in the laboratory. Craigieburn geckos may have been experiencing an unusually warm summer, or conversely, Banks Peninsula geckos may have experienced an unusually cool summer, leading to higher observed PBT in Craigieburn geckos. However, weather conditions recorded near both sites prior to sampling were characteristic of their respective areas over the summer of 1991 (Tocher 1992, pers. comm. Christchurch Meteorological Office; pers. comm. T. McSeveny, Soil & Plant Processes, Land Care Researcg, New Zealand Ltd.). Similarly, winter conditions were not abnormal for either site (pers. comm. T. McSeveny). During collection Craigieburn geckos were dormant, with snow 1 m deep in places. Conversely, Banks Peninsula geckos were visibly active in crevices at the same time of year (July). Thus, weather conditions appear unable to explain this paradoxical elevation of PBT in Craigieburn geckos.

Studies by Patterson & Davies (1978), and Van Damme *et al.* (1986, 1987) have shown a differentiation between observed PBT in different age and sex classes of the lizard *Lacerta vivipara*. Patterson & Davies (1978) found that adult male *L. vivipara* tended to have higher PBTs during cold months, which coincided with spermatogenesis. Spermatogenesis is known to be temperature dependent in (some) reptiles (Joly & Saint Girons 1981). Therefore, it is possible that the high PBT found for Craigieburn males after both cold temperature acclimation, and when collected in winter, may be related to spermatogenesis. In support, McIvor (1972) investigated the reproductive biology of a population of *H. maculatus* on Quail Island, Lyttelton Harbour (Christchurch, New Zealand). Spermatogenesis was found to occur in autumn (April-June), with spermatids maturing over the winter period. Robinson (1985) also reports this for *H. maculatus*. For Craigieburn geckos (in comparison to Banks Peninsula) the activity season is greatly shortened and males may be forced to expose themselves to unfavourable conditions and devote a considerable amount of time to activities that elevate their body temperatures to aid in spermatogenesis and sperm maturation. These activities may increase sexual encounters in the autumn (McAvoy 1976, Robinson 1986) and ultimately increase mating success. Furthermore, mating success in *L. vivipara* is known to be greatest in males which emerge earliest from hibernation (Bauwens & Verheyen 1985) and early emergence in Craigieburn males may be aided by an inherently high PBT during hibernation.

The above discussion suggests possible strategies employed by Craigieburn geckos that might account for the possible elevated PBT in cold acclimated geckos and the elevation in geckos collected in winter. However, the relatively high PBT of Craigieburn geckos after warm acclimation and after collection from the field in summer requires further explanation.

Banks Peninsula geckos probably experience warmer temperatures more frequently than geckos from Craigieburn and therefore have a greater chance of exposure to relatively high tem-

peratures (see Tocher 1992). Such exposure may have led to the development of mechanisms to avoid overheating and perhaps even death; mechanisms analogous to those employed by 'shuttling heliotherms'. Shuttling heliotherms maintain body temperature within certain bounds during activity by behaviourally shuttling between sunlight and areas of shade (DeWitt 1963, Mayhew 1963). Geckos from Craigieburn, on the other hand, may have lost or never developed such safety measures. It may be that long-term exposure to a higher PBT in Banks Peninsula geckos would result in 'metabolic burn-out', testicular damage (Wilhoft & Anderson 1960), spinal deformities (pers. obs.), or even death. Support for this hypothesis comes from work on the thermophilic species *Sceloporus occidentalis* (Wilhoft and Anderson 1960). After exposure to constant high temperatures these workers reported a decline (*ie.* 'reverse' acclimation) in the mean body temperature selected in the laboratory. This result was unexplained, but may be a mechanism to avoid so-called 'metabolic burnout'.

The higher PBT of Craigieburn geckos in both acclimation and acclimatization treatments may, alternately, be a case of not knowing when to say 'no', or due to an inability to use those behavioural techniques available in the wild to thermoregulate. Without appropriate 'switching off' mechanisms geckos may attempt to raise body temperature to unrealistically high levels, much higher than would be encountered naturally.

A more likely explanation for observed difference in PBTs between populations relates to the climatic regimes experienced at each site during the summer. It is accepted that *H. maculatus* basks during the day within sheltered sites (Werner & Whitaker 1978, pers. obs.), or utilises favourable microclimates by moving from deeper retreats to more exposed sites (pers. obs.). The relatively high PBT of Craigieburn geckos in summer (and after 25°C acclimation) may enable activity to continue longer through the night than would otherwise be possible with a lower PBT. Support for this view has been provided by Grimmond & Evetts (1980), who found that the body cooling rate of *H. maculatus* was much slower than body heating rate. Therefore, maximising stored heat load could be a profitable strategy for geckos at the Craigieburn site where nightly air temperatures can drop rapidly, and where duration of time that high temperatures are avaliable may be relatively short in comparsion to Banks Peninsula.

Further research is required on the relationship of physiological and ecological functions to PBT in each of these populations before the significance of this result can be determined. However, the consistency of the result is rather intriguing.

In summary, geckos collected in summer and winter from Banks Peninsula and Craigieburn show differences in their respective PBTs. Geckos from Craigieburn have higher PBTs than geckos from Banks Peninsula in both seasons. Both populations have a lower PBT in winter than in summer. This provides evidence of acclimatization of PBT with winter field conditioning inducing a drop in PBT.

Acclimation to laboratory conditions of constant temperature and 12L:12D light regime brought about similar changes in PBT as summer/winter treatments *ie.* treatment to 'warm' conditions produced a high PBT, whilst 'cold' treatment produced a lower PBT.

Paradoxically, Craigieburn geckos exhibited a consistently higher PBT than Banks Peninsula geckos, significant only for acclimatized geckos.

ACKNOWLEDGEMENTS

I thank Dr. Bill Davison and Raphael Didham for useful comments on this manuscript.

REFERENCES

Arnold, E. & Gallagher M.D. (1977). Reptiles and amphibians from the mountains of Northern Oman. *Jounal of Oman Studies Special Report* 1: 59-79.

Bartholomew, G.A. (1982). Physiological control of body temperature. In *Biology of the Reptilia*, Vol. 12, (eds. Gans & Pough), pp. 167-211. Academic Press, London.

Bauwens, D. & Verheyen, R.F. (1985). The timing of reproduction in the lizard *Lacerta vivipara*: differences between individual females. *Journal of Herpetology* 19: 353-364.

Bogert, C.M. (1949). Thermoregulation in reptiles, a factor in evolution. *Evolution* 3: 195-211.

Brattstrom, B.H. (1965). Body temperatures of reptiles. *American Midland Naturalist* 73: 377-422.

Brown, J.H. & Feldmuth, C.R. (1971). Evolution in constant and fluctuating environments: thermal tolerances of the desert pupfish (*Cypinidon*). *Evolution* 25: 390-398.

Bullock, T.H. (1955). Compensation for temperature in the metabolism and activity of poikilotherms. *Biological Reviews* 30: 311-342.

Bustard, H.R. (1967). Activity cycle and thermoregulation in the Australian gecko *Gehyra variegata*. *Copeia* 1967: 753-758.

Cogger, H.G. (1974). Thermal relations of the Mallee Dragon *Amphibolurus fordi* (Lacertilia: Agamidae). *Australian Journal of Zoology* 22: 319-339.

Cowles, R.B. & Bogert, C.M. (1944). A preliminary study of the thermal requirements of desert reptiles. *Bulletin. American Museum of Natural History* 83: 265-296.

Crowley, S.R. (1985). Thermal sensitivity of sprint-running in the lizard *Sceloporus undulatus*: support for a conservative view of thermal physiology. *Oecologia* (Berl.) 66: 219-225.

Dawbin, W.H. (1962). The Tuatara in its natural habitat. *Endeavour* 21: 16-24.

Dawson, W.R. (1960). Physiological responses to temperature in the lizard *Eumeces obsoletus*. *Physiological Zoology* 33: 87-103.

Dawson, W.R. (1967). Interspecific variation in physiological responses of lizards to temperature. In *Lizard ecology: a symposium*, (ed. W.W. Milstead), pp. 230-257. University of Missouri Press, Missouri.

Dawson, W.R. (1975). On the physiological significance of the preferred body temperatures of reptiles. In *Perspectives in Biophysical Ecology*, (eds. D.M. Gates and R.B. Schmerl), pp. 443-473. Springer-Verlag, New York.

Dawson, W.R. & Bartholomew, G.A. (1958). Metabolic and cardiac responses to temperature in the lizard *Dipsosaurus dorsalis*. *Physiological Zoology* 31: 100-111.

Dawson, W.R. & Templeton, J.R. (1963). Physiological responses to temperature in the lizard *Crotaphytus collaris*. *Physiological Zoology* 36: 219-236.

Dawson, W.R. & Templeton, J.R. (1966). Physiological responses to temperature in the alligator lizard, *Gerrhonotus multicarinatus*. *Ecology* 47: 759-765.

DeWitt, C.B. (1963). Behavioural thermoregulation in the iguanid lizard, *Dipsosaurus dorsalis*. Unpublished Ph.D. Thesis, University of Michigan, USA.

DeWitt, C.B. (1967). Precision of thermoregulation and its relation to environmental factors in the desert iguana, *Dipsosaurus dorsalis*. *Physiological Zoology* 40: 49-66.

Grimmond, N.M. & Evetts, P.M. (1980). The effects of temperature on heat exchange and oxygen consumption in two sympatric New Zealand lizards. In *Advances in physiological sciences, Vol. 32: Contributions to thermal physiology*, (eds. Szelenyi & Szekely), pp. 257-259. Satellite symposium of the 28th International Congress of physiological sciences. Pecs, Hungary. Akademiai Kiado, Budapest, Hungary.

Hardy, G.S. (1971). The effects of light and temperature on daily activity in the gecko *Hoplodactylus pacificus*. Unpublished BSc. (Hons) thesis, Victoria University of Wellington, New Zealand.

Heatwole, H. (1970). Thermal ecology of the desert dragon *Amphibolurus nermis*. *Ecological Monographs* 40: 425-457.

Huey, R.B. (1982). Temperature, physiology, and the ecology of Reptiles. In *Biology of the Reptilia*. Vol.12 (eds. Gans & Pough), pp. 25-91. Academic Press, London.

Huey, R.B. & Slatkin, M. (1976). Costs and benefits of lizard thermoregulation. *Quart.erlyReview of Biology* 51: 363-384.

Joly, J. & Saint-Girons, H. (1981). Influence de la temperature sur la vitesse de la spermatogenese de *Lacerta vivipara* et comparsion avec *Lacerta muralis* (Reptilia: Lacertidae). *Bulletin. Societe Zoologique de France* 106: 337-340.

Kaufmann, J.S. & Bennett, A.F. (1989). The effect of temperature and thermal acclimation on locomotor performance in *Xantusia vigilis*, the desert night lizard. *Physiological Zoology* 62: 1047-1058.

Licht. P. (1964). The relation between thermoregulation and physiological adjustments to temperature in lizards. Unpublished Ph.D. Thesis, University of Michigan, USA.

Licht, P. (1965). The relation between body temperatures and testicular heat sensitivity in lizards. *Copeia* 1965: 428-436.

Licht, P. (1967). Thermal adaptation in the enzymes of lizards in relation to preferred body temperatures. In *Molecular mechanisms of temperature adaptation*, (ed. C.L. Prosser), pp. 131-145. Washington: American Association for the advancement of science, Publication No. 84.

Licht, P. (1968). Response of the thermal preferendum and heat resistance to thermal acclimation under different photoperiods in the lizard *Anolis carolinensis*. *American Midland Naturalist* 79: 149-158.

Licht, P., Dawson, W.R. & Shoemaker, V.H. (1969). Thermal adjustments in cardiac and skeletal muscles of lizards. *Z. Vergleich. Physiol.* 65: 1-14.

Licht, P., Dawson, W.R., Shoemaker, V.H. & Main, A.R. (1966). Observations on the thermal relations of Western Australian lizards. *Copeia* 1966: 97-110.

McGinnis, S.M. (1966). *Sceloporus occidentalis*: preferred body temperature of the western fence lizard. *Science* 152: 1090-1091.

McIvor, I.R. (1972). Ecology of a population of *Hoplodactylus pacificus*, the common New Zealand gecko. Unpublished MSc. thesis, University of Canterbury.

Mayhew, W.W. (1963). Temperature preferences of *Sceloporus orcutti*. *Herpetologica* 18: 217-233.

MacAvoy, E.S. (1976). The physiology of lizards from arid regions in Central Otago. Unpublished PhD thesis, University of Otago, New Zealand.

Mellish, C.H. (1936). The effects of anterior pituitary extract and certain environmental conditions on the genital system of the horned toad (*Phrynosoma cornutum* Harlan). *Anat.omicalRecord.* 67: 23-33.

Patterson, J.W. & Davies. P.M.C. (1978). Preferred body temperature: seasonal and sexual differences in the lizard, *Lacerta vivipara*. *Journal of Thermal Biology* 3: 39-41.

Pianka, E.R. & Pianka, H.D. (1976). Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the Western Australian desert. *Copeia* 1976: 125-142.

Regal, P. (1966). Thermophilic response following feeding in certain reptiles. *Copeia* 1966: 588-590.

Robinson, M. (1985). Sexual cycles of New Zealand lizards, with particular reference to the gecko *Hoplodactylus maculatus* (Boulenger). Unpublished MSc thesis, Victoria University of Wellington New Zealand.

Templeton, J.R. (1970). Invertebrates & non-mammalian vertebrates. In *Comparative physiology of thermoregulation* (ed. Whittow), pp. 167-221, New York: Academic Press.

Tocher, M.D. (1992). The New Zealand common gecko *Hoplodactylus maculatus*: an ecophysiological comparison of two isolated populations. Unpublished MSc. thesis, University of Canterbury, New Zealand.

Tsuji, J.S. (1988). Thermal acclimation of metabolism in *Sceloporus* lizards from different latitudes. *Physiological Zoology* 61: 241-253.

Van Berkum, F.H. (1986). Evolutionary patterns of the thermal sensitivity of sprint speeds in *Anolis* lizards. *Evolution* 40: 594-604.

Van Damme, R., Bauwens, D. & Verheyen, R.F. (1986). Selected body temperatures in the lizard *Lacerta vivipara*: variation within and between populations. *Journal of Thermal Biology* 11: 219-222.

Van Damme, R., Bauwens, D. & Verheyen, R.F. (1987). Thermoregulatory responses to environmental seasonality by the lizard *Lacerta vivipara*. *Herpetologica* 43: 405-415.

Van Damme, R., Bauwens, D. & Verheyen, R.F. (1990). Evolutionary rigidity of thermal physiology: the case of the cool temperate lizard *Lacerta vivipara*. *Oikos* 57: 61-67.

Werner, Y.L. (1965). Uber die israelischen Geckos der Gattung *Ptyodactylus* und ihre Biologie. *Salamandra* 1: 15-25.

Werner, Y.L. (1966). *Cyrtodactylus kotschyi orientalis* in Israel. *Lacerta* 24: 94-96.

Werner, Y.L. (1972). Temperature effects on inner ear sensitivity in six species of iguanid lizards. *Journal of Herpetology* 6: 147-177.

Werner, Y.L. & Whitaker, A.H. (1978). Observations and comments on the body temperatures of some New Zealand reptiles. *New Zealand Journal of Zoology* 5: 375-393.

Wilhoft, D.C. & Anderson, J.D. (1960). Effect of acclimation on the preferred body temperature of the lizard, *Sceloporus occidentalis*. *Science* 131: 610-611.